

Anatomy of an Invasion: Systematics and Distribution of the Introduced Opisthobranch Snail, *Haminoea japonica* Pilsbry, 1895 (Gastropoda: Opisthobranchia: Haminoeidae)

Terrence M. Gosliner and David W. Behrens

California Academy of Sciences, 875 Howard Street, San Francisco, CA 94103;

Email: tgosliner@calacademy.org, dwbbehrens@comcast.net

Haminoea japonica Pilsbry, 1895 is documented from the Pacific coast of North America and from European waters in Italy and northwestern Spain. *Haminoea japonica* is a senior synonym of *Haminoea callidegenita* Gibson & Chia, 1989, which was originally described from the coast of Washington. Subsequently, it was reported from European waters as *H. callidegenita*. The present study examines material collected from San Francisco Bay and compares it with material collected from two localities in Japan. Anatomical similarities in the external anatomy, coloration, radula, jaw, gizzard and reproductive anatomy demonstrate that the specimens represent a single conspecific species. *Haminoea japonica* has priority over *H. callidegenita*.

Haminoea callidegenita was first recorded from Lopez Island and Rock Point, Samish Bay both in Washington State (Gibson and Chia 1989). In the original description, it was noted that specimens had come from commercial, non-native oyster beds and that the species may be introduced. The authors completely described the anatomy of their new species and stated that their comparison with other described species of *Haminoea* did not find any species with similarly known anatomy. Their efforts were certainly hampered by incomplete anatomical information for many species, as the vast majority of Haminoeidae is known only from empty shells. Following the original description of this species, Álvarez et al. (1993b) recorded additional specimens from northwestern Spain and Venice, Italy. The opisthobranchs were associated with introduced Manila clams, *Ruditapes philippinarum* (Adams and Reeve, 1850).

In September of 1999, as part of the initial surveys for the San Francisco Bay2K project of the California Academy of Sciences, field work was conducted at several localities within San Francisco Bay. During surveys at Brisbane Harbor just south of San Francisco, several specimens of a previously undetected species were detected. These were examined anatomically and compared with Gibson and Chia's description of *H. callidegenita*. The specimens agreed with this species in all respects. From a search of the literature for other species from other geographical regions that might also resemble the present material, a publication of Habe (1952) included an illustration of the radula of what he called *Haloa rotundata* (A. Adams, 1850) that was similar to the present material. In subsequent works (Habe 1961; Hori 2000) there has been no reference to *H. rotundata* but rather the name *Haloa japonica* appears. It seems that Japanese authors now consider what Habe originally reported as *H. rotundata* to be *H. japonica*. Since that time, we have been able to secure material of this species from Japan to compare with specimens from San Francisco Bay. Early in 2006, specimens from Japan had been collected and sent to us. The present work represents a comparison of the anatomy of specimens from Japan with material from San Francisco Bay.

Haminoea japonica Pilsbry, 1895

Haminea binotata var. *japonica* Pilsbry, 1895:185.

?*Halooa rotundata* (A. Adams) Habe, 1952:149, text fig. 4, pl. 20, fig. 4, pl. 21, fig. 24.

Haminoea callidegenita Gibson & Chia, 1989:914, figs. 1-8, **syn. nov.**

MATERIAL EXAMINED.— CASIZ 066897, one specimen, dissected, rocky tide pools, Shinnase, Hayama, Sagami Bay, Japan, 4 June, 1970, F. Steiner. CASIZ 174123, eight specimens, two dissected, from floating docks, Brisbane Marina, Brisbane, San Francisco Bay, 5 September 2000, T. Gosliner, R. Van Syoc, R. Mooi, M. Burke. CASIZ 174124, 18 specimens, one dissected, boat launch ramp, Lake Merritt Boat Club, Oakland, San Francisco Bay, California, 1 November, 2003, S. Behrens. CASIZ 172021, one specimen, Kotsubo, Sagami Bay, Japan, March 2005, Y. Sato. CASIZ 174125, 5 specimens, one dissected, intertidal zone, Hachijo Island, Japan, June 2004, H. Takasu.

EXTERNAL ANATOMY.— The preserved specimens are up to 20 mm in length. In living specimens (Figs. 1A, B) the headshield is lobed and rounded anteriorly with elongate, rounded, deeply divided posterior lobes. The ground color is translucent white with scattered opaque white spots and a dense covering of dark brown spots that are most dense on the center of the headshield and on the short parapodia lobes, which partially envelop the yellowish, transparent shell. A posterior mantle lobe with brown and opaque white bands partially covers the posterior end of the shell. A long, rounded posterior end of the foot extends posteriorly from the shell. Through the transparent shell, the translucent white mantle is covered with large brown spots and scattered bright orange spots.

DIGESTIVE SYSTEM ANATOMY.— The buccal mass is large and muscular. At the anterior end of the mass is a pair of chitinous jaws that bear a series of irregular, polygonal rodlets (Fig. 2). More posteroventrally, the radula is situated within the buccal mass. The radular formula is $22 \times 14-16.1.14.16$ (CASIZ 174123, Brisbane), $28 \times 14-16.1.14-16$ (CASIZ 174124, Lake Merritt), $23 \times 14-15.1.14-15$ (CASIZ 174125, Hachijo Island) and $23 \times 14-15.1.14-15$ (CASIZ 066897, Sagami Bay). In all cases, the rachidian row bears teeth with a broad base that are tricuspid (Fig. 3) with relatively short lateral cusps. The inner lateral teeth (Fig. 3) are elongate with a large primary cusp and a single rounded denticle situated on the inner side of the primary cusp. The middle and outer lateral teeth (Fig. 4) are simple and elongate with an elongate cusp that is devoid of denticulation. The lateral teeth increase from the rachis to the middle of the half-row and decrease again towards the outer margin of the radula. Posterior to the buccal mass is the muscular gizzard that contains three large chitinous plates of equal size and symmetrical shape. Each plate is ornamented with 11–12 v-shaped lateral ridges (Figs. 5A–D). Each ridge bears a series of numerous elongate spines (Figs. 5E–F).

REPRODUCTIVE ANATOMY.— The hermaphroditic reproductive system is monaulic. From the genital opening near the opening of the mantle cavity, an elongate sperm groove. The sperm groove continues anteriorly along the right side of the body to the opening of the penis. The penis (Fig. 6) consists of an oblong, glandular prostatic bulb followed that narrows into a muscular ejaculatory duct that is convoluted. The ejaculatory duct enters the elongate penial bulb, which is wide and elongate. The bulb is wide and has a muscular lining. Microscopic examination of two specimens (CASIZ 174123, Brisbane and CASIZ 066897, Sagami Bay, Japan) by means of staining and clearing of the specimens revealed the ejaculatory duct and penial bulb entirely lack any spines. The lining of the ejaculatory duct is ciliated but unarmed. The base of the penis lacks a distinct penial papilla.

DISCUSSION

Haminoea is considered to include about 70 species, most of which are known only from char-



FIGURE 1. Living animal A, CASIZ 174123 from Brisbane, San Francisco Bay, photo by T. Gosliner. B. CASIZ 172021, Sagami Bay, Japan, photo by Yukari Sato.

acteristics of the shell (Rudman 1971). Since Rudman's review, at least four additional species have been named (Talavera et al. 1987; Gibson and Chia 1989; García et al. 1991; Álvarez et al. 1993a).

Haminoea binotata var. *japonica* was described by Pilsbry (1895) from a single specimen collected from Nemoto, Boshu, Japan. Nemoto is situated at the southern tip of the Boso Peninsula

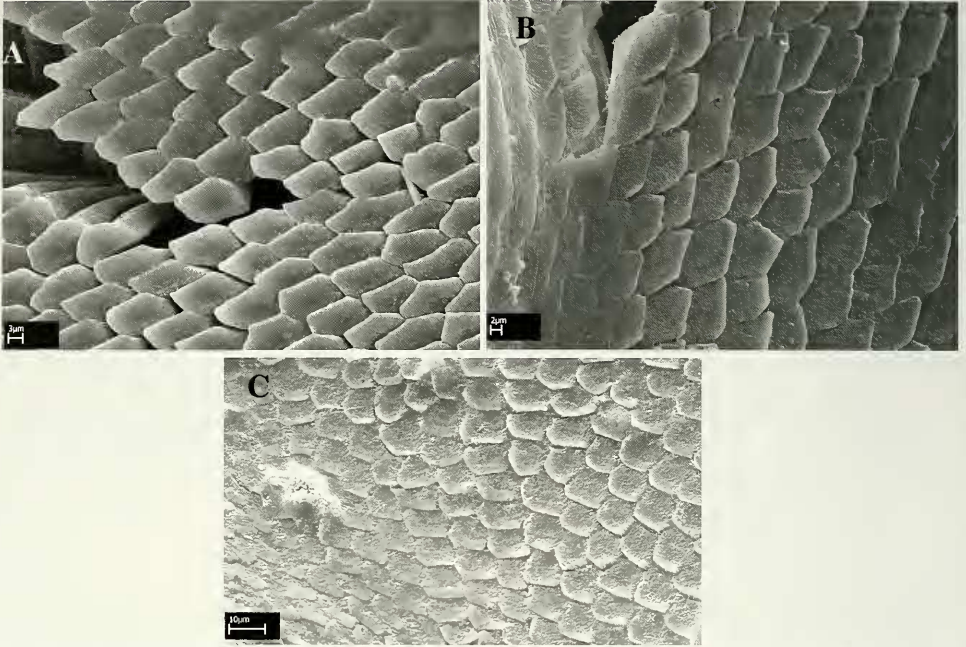


FIGURE 2. Jaw rodlets. A. CASIZ 174124, Lake Merritt, San Francisco Bay; scale bar = 3µm. B. CASIZ 174125, Hachijo Island, Japan; scale bar = 2µm. C. CASIZ 066897, Sagami Bay, Japan; scale bar = 10µm.

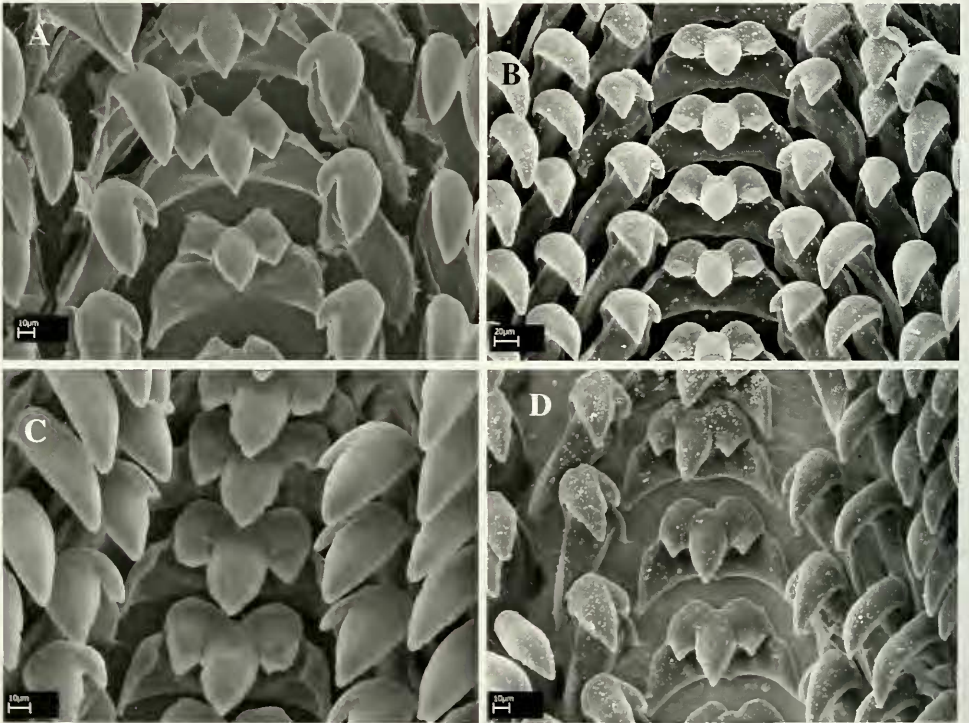


FIGURE 3. Central portion of radula. A. CASIZ 174123, Brisbane; scale bar = 10µm. B. CASIZ 174124, Lake Merritt; scale bar = 20µm. C. CASIZ 174125, Hachijo Island; scale bar = 10µm. D. CASIZ 066897, Sagami Bay; scale bar = 10µm.

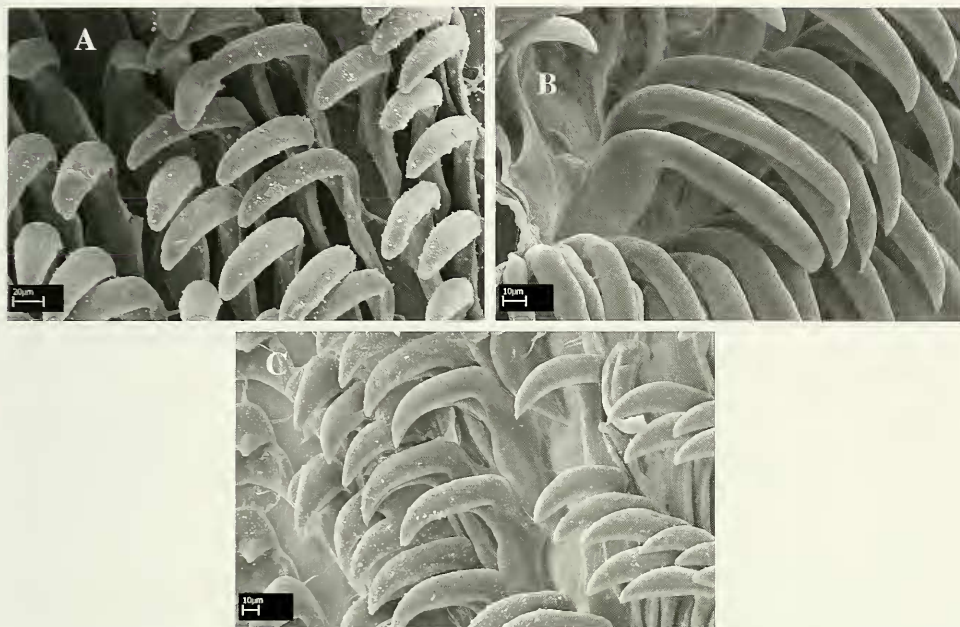


FIGURE 4. Outer lateral teeth. A. CASIZ 174123, Lake Merritt; scale bar=20µm. B. CASIZ 174125, Hachijo Island; scale bar = 10µm. C. CASIZ 066897, Sagami Bay; scale bar = 10µm.

that forms the eastern boundary of Sagami Bay. The specimen was not illustrated, but was described as smaller, more fragile and with a more swollen shell with a thinner collumellar callus than the typical *H. binotata*. Habe (1952) considered this variety as a synonym of *H. binotata*, but later (1961) considered it as a distinct species. Habe (1952, pl. 21, fig. 24) depicted the radula of what he called *Haloa rotundata* (A. Adams, 1850). This species has a tricuspid rachidian tooth with an inner lateral tooth bearing a single denticle on the inside of the primary cusp. In subsequent works, Habe and other subsequent Japanese workers refer only to *Haloa japonica* but not to *H. rotundata*. Although, we were unable to find any specific reference to this exclusion of *H. rotundata* and usage of *H. japonica*, it appears that this was based on the recognition of the Japanese specimens as being distinct from *H. rotundata*, originally described from the Philippines. The name *Haloa japonica* has remained in common usage in Japanese malacological catalogs to the present (Hori 2000).

Pilsbry (1920) divided the genus *Haminoea* into three sections, *Haminoea*, *Haloa* and *Liloa* based on conchological differences. Habe (1952) stated that a distinguishing feature of *Haloa* was the presence of a denticle on the inner side of the inner lateral tooth, based on his examination of *H. rotundata* (probably = *H. japonica*, see above), Rudman (1971) noted that the type species of *Haloa*, *H. crocata* (Pease, 1868), lacks this characteristic of the inner lateral tooth. Rudman also noted that he could not discern any of the conchological distinctions noted by Pilsbry and united these taxa under *Haminoea*. This synonymy has been ignored by some subsequent workers (see Hori 2000).

The description of *Haminoea callidegenita* Gibson and Chia, 1989 represents the first detailed description of a new species of *Haminoea* recorded from the Pacific coast of North America. This species is clearly distinct from the two other valid species found in the temperate eastern Pacific, *Haminoea vesicula* Gould, 1855 and *H. virescens* Sowerby, 1833 (Gibson and Chia 1989). Externally, *H. callidegenita* has deeply divided posterior lobes of the headshield while those of the other two species are only shallowly notched. Gibson and Chia also noted significant radular and

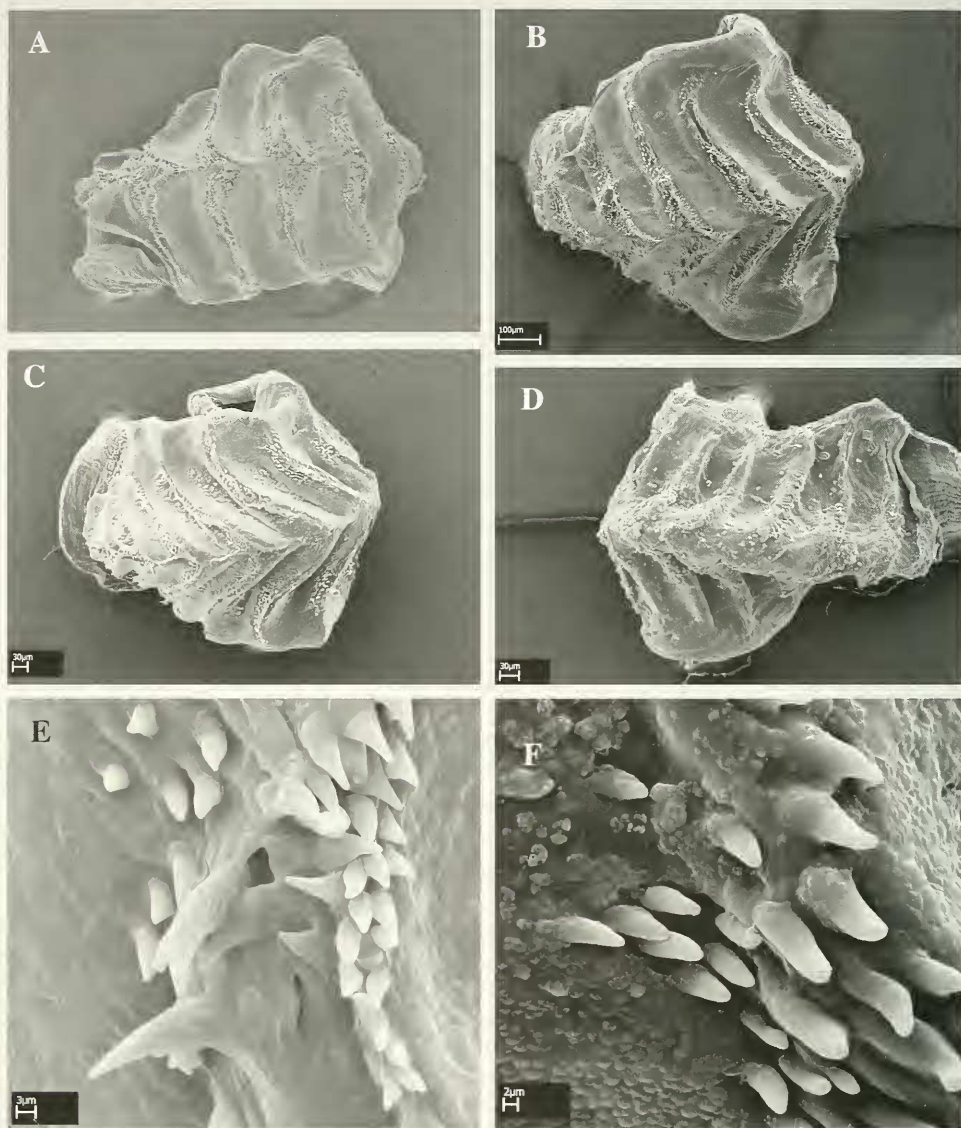


FIGURE 5 Gizzard plates. A. Gizzard plate, CASIZ 174123, Brisbane; scale bar = 100µm. B. Gizzard plate, CASIZ 174124, Lake Merritt; scale bar = 100µm. C. Gizzard plate, CASIZ 174125, Hachijo Island; scale bar = 30µm. D. Gizzard plate, CASIZ 066897, Sagami Bay; scale bar = 30µm. E. Ridge ornamentation, CASIZ 174124, Lake Merritt; scale bar = 3µm. F. Ridge ornamentation, CASIZ 174125, Hachijo Island; scale bar = 2µm.

penial differences among the three species. The inner lateral teeth of *H. callidegenita* have a single rounded denticle on the inside of the primary cusp, while those of *H. virescens* and *H. vesicula* are either smooth or denticulate (with many denticles). The penial morphology also differs and *H. callidegenita* is unique among the three in having a single elongate prostate, while that of *H. vesicula* has a bilobed prostate and that of *H. virescens* has a spherical prostate with a much thicker penial bulb.

The anatomy of *H. callidegenita* from Europe (Álvarez et al. 1993b) closely matches that of Gibson and Chia's and there is little doubt that this represents the same species. The likelihood that

the same species was found in Washington State and in two localities in Europe in association with Japanese shellfish culture prompted us to compare specimens of *H. callidegenita* with species known from Japan. The discovery of specimens of *H. callidegenita* from San Francisco Bay provided that opportunity.

As stated previously, Habe's (1952) depiction of the radula of what he called *H. rotundata* (probably *H. japonica*) closely matched that of *H. callidegenita*. More importantly, of the approximately 15 species of *Haminoea* whose radular morphology is described, only Habe's animal and *H. callidegenita* are known to possess an inner lateral tooth with a single denticle present inside the primary cusp. Two other described species of *Haminoea* have a prostate and penial shape similar to the present material from California and Japan. In *H. linda* Marcus & Burch, 1965, the prostate is oblong as in *H. japonica*, but the ejaculatory duct bears small spines within its lining that are absent in *H. japonica* (Marcus & Burch, 1965). In *H. solitaria* (Say, 1822), the prostate is oblong but the base of the penial bulb is armed with spines (Marcus 1972).

Gibson and Chia (1989) noted that the eggs of *Haminoea callidegenita* were yellow in color, approximately 230 μm in diameter and produced both lecithotrophic and direct developing individuals from the same egg mass. Ito (1997) described aspects of the developmental biology of *Haloa japonica* from Japanese populations. He noted that the egg masses contained yellow eggs that ranged in diameter between 259–289 μm and developed into lecithotrophic veligers. There are great similarities in that both have yellow eggs of similar sizes that undergo lecithotrophic development and in the case of the specimens from Washington also include some direct developing individuals. The vast majority of species of *Haminoea* that have been studied have planktotrophic development and have eggs that are white in color (present study). Thus, specimens of *H. callidegenita* and *H. japonica* have similar life histories and developmental characteristics that are unusual for members of *Haminoea*.

With the acquisition of specimens of *H. japonica* from Japan, it was possible to make detailed anatomical comparisons between North American and Japanese specimens. The fact that two of these specimens were collected from Sagami Bay, very close to the type locality of *H. japonica*, further increases the likelihood that they are conspecific with Pilsbry's poorly described species. All of the anatomical features examined are in complete accord and there is no doubt that the two species are conspecific with *H. japonica* having priority over *H. callidegenita*. *Haminoea callidegenita* is therefore regarded as a junior synonym of *H. japonica*. Thus, it appears that *H. japonica* has been introduced to the Pacific coast of North America and to Europe with the introduction of Japanese oysters and clams for maricultural purposes.

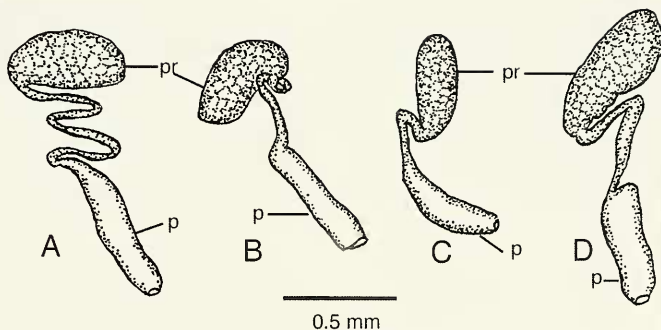


FIGURE 6. Penial morphology. A. CASIZ 174123, Brisbane. B. CASIZ 174124, Lake Merritt. C. CASIZ 066897, Sagami Bay, Japan. D. CAS 174125, Hachijo Island, Japan. Key: p = penial bulb; pr = prostate.

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